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GEOGRAPHICAL DISTRIBUTION OF BRACHYSTOMELLINAE (COLLEMBOLA: NEANURIDAE)

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Abstract.—The subfamily Brachystomellinae, Collembola, currently includes 14 genera occurring mostly on the Southern Hemisphere with the sole exception of *Brachystomella,* which is distributed worldwide. The genera *Bonetella, Salvarella* and *Subclavontella* are endemic for Australia. *Rapoportella* occurs primarily in the Neotropical region, with a single species known from the Australian region, although *Cassagnella,* reported also from the southern part of South America, is well developed in Australia. *Brachystomellides* and *Setanodosa* are represented in the Neotropical and the Australian regions. The other five genera: *Micronella, Parastomella, Raponella, Winterella* and *Folsomiella* occur exclusively in the Neotropical region. *Probrachystomellides* is distributed in the Ethiopian region. Thus, both the greatest number of genera (as many as 10), and maximum species diversity (57 species), are to be found in the Neotropical regions.

Key Words.—Insecta, Collembola, Brachystomellinae, biogeography, zoogeographic regions

TAXONOMIC CONSIDERATIONS

The subfamily Brachystomellinae is distributed on all continents and includes 15 genera: *Bonetella* Stach, 1949; *Brachystomella* Agren, 1903; *Brachystomellides* Arlé, 1959; *Cassagnella* Najt & Massoud, 1974; *Folsomiella* Bonet, 1930; *Massoudella* (= *Australella,* Stach, 1949), Ellis & Bellinger, 1973; *Micronella* Arlé, 1959; *Parastomella* Rapoport & Rubio, 1968; *Probrachystomellides,* Weiner & Najt, 1991; *Raponella* Najt, 1988; *Rapoportella* (= *Probrachystomella* Rapoport, 1962) Ellis & Bellinger, 1973; *Salvarella* Greenslade & Najt, 1987; *Setanodosa* Salmon, 1942; *Subclavontella* Stach, 1949; and *Winterella* Massoud, 1967. A dubious genus, *Guacharia* Jackson, 1927, similar to *Brachystomella* with seven ocelli was distinguished on the basis of immature specimens (Type species: *G. trinitata* = *B. septemoculata* Denis, 1931?).

We examined types of brachystomelline species from the collection of the National Museum of Natural History in Paris, and concluded that some of the genera contain species which are either transitional or difficult to classify as belonging to one of the closely related genera. Thus, within one population of *Brachystomella surendrai* Goto, 1961, specimens may have normal or reduced mucro. *Brachystomella minimucronata* Palacios-Vargas & Najt, 1981 has its mucro strongly reduced and *Brachystomella cyanea* (Rapoport, 1962) has the whole furca reduced to two mamelons. *Brachystomella emder* Greenslade & Najt, 1987 possesses all characters of the genus but it is the only species known so far with spiniform setae on dens, which is typical of the genus *Brachystomellides.*

Among the species of the genus *Brachystomellides,* only *B. neuquensis* Cassagnau & Rapoport, 1962, has globular maxillae with numerous teeth, as found in the genus *Brachystomella*; the remaining three species have a globular maxilla with only one or two teeth. *Winterella arlesiana* Massoud, 1967, has a pair of reduced mandibles, without a molar plate. This is a primitive character, which also occurs in *Probrachystomellides nicolaii* Weiner & Najt, 1991. In all other genera the mandibles are absent.

As regards chaetotaxy, most of the genera demonstrate a distinct paurochaetosis. Plurichaetosis is developed only in three genera: less conspicuously in *Cassagnella,* abundantly in *Bonetella* and *Salvarella.*

Massoudella and *Brachystomellides* are identical in all generic characters, including the presence of crosier-like structures on labium, as described by Massoud, 1967. For this reason we propose the following synonymy: *Brachystomellides* = *Massoudella* syn. nov. Consequently, the subfamily Brachystomellinae should contain 14 genera.

To better understand the geographical distribution of this group we have performed a phylogenetic analysis based on morphological characters (to be published separately), the results of which were applied in this work. The analysis enabled us to distinguish two sister lineages: brachystomellian and rapoportellian groups, each descended from a common ancestor.

Geographic Distribution.—In 1967 Massoud presented an outline of the geographic distribution for ten genera of Brachystomellinae. The principal lineage includes five genera, *Brachystomella, Folsomiella, Setanodosa, Micronella* and *Winterella,* and gives rise to two Neotropical lineages: one with *Rapoportella,* the other with *Brachystomellides.* The fourth lineage, exclusively Australian, includes three genera: *Subclavontella, Bonetella* and *Massoudella.*

Rapoport (1971) published a study of the geographical distribution of Neotropical and Antarctic Collembola, considering only a few representatives of Brachystomellinae. The author postulated that *Folsomiella, Micronella, Parastomella, Brachystomellides, Winterella* and *Rapoportella* were endemic to the Neotropical region. The occurrence of *Brachystomellides neuquensis* in Argentina and Chile and the discovery of a new (although not described) species from this genus in Peru (Winter 1962) gave evidence of the existence of contacts between the two major stocks: Paleantarctic (relegated to the Araucanian subregion) and Neotropical (probably Afro-Brazilian or Holotropical). The genus *Brachystomella* was reported to occur commonly in two regions: Palaearctic and Neotropical, but Rapoport apparently overlooked its occurrence in the Australian region. *Setanodosa* is distributed in two regions: Australian and Neotropical. Rapoport considered the Holotropical region as the whole space between the tropics of Cancer and Capricorn, claiming that *Brachystomella contorta* Denis, 1931 was widely distributed over this vast area.

More than twenty years have passed since the publication of the two papers, which discussed, among other things, the distribution of Brachystomellinae. New genera and new species have since been described and the way in which their characters are analyzed has changed and with more attention paid to chaetotaxy. We re-examine the geographical distribution of genera and of species using the zoogeographic division of continents by Mroczkowski (1968). However, we note that, even today, the available data are fragmentary.

Table 1. Geographic distribution of the genera Brachystomellinae. Zoogeographic regions: Nea—Nearctic; Pal—Palearctic; Neo—Neotropical; Eth—Ethiopian; Ori—Oriental; Aus—Australian.

Genus	Nea	Pal	Neo	Eth	Ori	Aus
Bonetella Stach, 1949						+
Brachystomella Agren, 1903	+	+	+	+	+	+
Brachystomellides Arlé, 1959			+			+
Cassagnella Najt & Massoud, 1974			+			+
Folsomiella Bonet, 1930			+			
Micronella Arlé, 1959			+			
Parastomella Rapoport & Rubio, 1968			+			
Probrachystomellides Weiner & Najt, 1991				+		
Raponella Najt, 1988			+			
Rapoportella Ellis & Bellinger, 1973			+			+
Salvarella Greenslade & Najt, 1987						+
Setanodosa Salmon, 1942			+			+
Subclavontella Stach, 1949						+
Winterella Massoud, 1967			+			

Zoogeography of Brachystomellinae

Distribution of Genera.—The distribution of the brachystomelline genera by geographic regions is presented in Table 1. Only *Brachystomella* occurs in all regions. *Folsomiella, Micronella, Parastomella, Raponella* and *Winterella* are known only from the Neotropical region. One genus: *Probrachystomellides* belongs to the South-African subregion in the Ethiopian domain. Three genera: *Bonetella, Salvarella,* and *Subclavontella* are Australian. The distribution of *Brachystomellides* and *Cassagnella* covers two regions: the Australian and the Neotropical. *Rapoportella* is principally a Neotropical genus, but it is found in the southern part of the Nearctic region. This is probably the result of a neotropical expansion to the north (Sonoran province, see map 1: Mroczkowski 1968) prior to the rise of the Mexican neovolcanic chain. *Rapoportella* is also represented in Australia. *Setanodosa* occurs in the Neotropical and the Australian. *Brachystomella* is the only genus with a wide distribution; all other genera are found only south of the Tropic of Cancer.

Distribution of Species.—The distribution of species is presented according to two sister groups (to be published separately).

The brachystomellian group contains ten genera: *Brachystomella, Setanodosa, Micronella, Probrachystomellides, Brachystomellides, Parastomella, Bonetella, Winterella, Subclavontella* and *Folsomiella.*

Brachystomella includes 52 know species (Table 2). *Brachystomella parvula* is a typically Palaearctic species, which is found in the Nearctic region. It is our opinion that all specimens from other parts of the world that have been identified as belonging to this species should be re-examined. *Brachystomella contorta* is dispersed in the Neotropical, the Ethiopian, the Oriental regions and in the Hawaiian subregion (Australian region).

The distribution of *Brachystomella platensis* is rather peculiar: originally de-

Table 2. Geographic distribution of species of the genus *Brachystomella*. Zoogeographic regions: Nea—Nearctic; Pal—Palearctic; Neo—Neotropical; Eth—Ethiopian; Ori—Oriental; Aus—Australian.

Species	Nea	Pal	Neo	Eth	Ori	Aus
Brachystomella Agren, 1903						
agrosa Wray, 1953			+			
baconaoensis Gruia, 1983			+			
barrerai Palacios-Vargas & Najt, 1981			+			
chilensis Rapoport & Rubio, 1965			+			
christianseni Massoud, 1965						+
coatesi Weiner & Najt, 1991				+		
contorta Denis, 1931			+	+	+	+
curvula Gisin, 1948		+				
cyanea (Rapoport, 1962)			+			
dianae Greenslade & Najt, 1987						+
disputa Greenslade & Najt, 1987						+
emder Greenslade & Najt, 1987						+
fungicola Womersley, 1933						+
gabrielae Najt & Palacios-Vargas, 1986			+			
georgensis Weiner & Najt, 1991				+		
globulosa Cassagnau & Rapoport, 1962			+			
grootaerti Najt, Thibaud & Jacquemart, 1991			+			
hawaiiensis Yosii, 1965						+
heo Christiansen & Bellinger, 1992						+
hiemalis Yosii, 1956		+				
honda Christiansen & Bellinger, 1988	+					
insulae Najt & Thibaud, 1988						+
kahakai Christiansen & Bellinger, 1992						+
kiko Christiansen & Bellinger, 1992						+
koreana Weiner & Najt, 1985		+				
mauriesi Thibaud & Massoud, 1983				+		
micromucronata Palacios-Vargas & Najt, 1981		+				
momona Christiansen & Bellinger, 1992						+
montebella Najt & Palacios-Vargas, 1986			+			
nana Rubio & Najt, 1979			+			
neomexicana (Scott, 1960)			+			
nubila Gisin, 1957		+				
parvula (Schaeffer, 1896)	+	+				
pastoralis Greenslade & Najt, 1987						+
perraulti Thibaud & Najt, 1993						+

Table 2. Continued.

Species	Nea	Pal	Neo	Eth	Ori	Aus
platensis Najt & Massoud, 1974			+			+
quadrituberculata Stach, 1964		+				
ronderosi Najt, 1973			+			
septemoculata Denis, 1931			+			
sexoculata Massoud, 1967			+			
solidaria Greenslade & Najt, 1987						+
stachi Mills, 1934	+		+			
subandinensis Massoud, 1967			+			
surendrai Goto, 1961					+	
taxcoana Palacios-Vargas & Najt, 1981			+			
terrafolia Salmon, 1944						+
tuberculata (Wahlgren, 1906)			+			
ultima Greenslade & Najt, 1987						+
unguilonga Najt & Thibaud, 1988						+
victoriensis Izarra, 1972			+			
villalobosi Cassagnau & Rapoport, 1962			+			
zapatai Najt & Palacios-Vargas, 1986			+			

scribed from an eucalyptus grove in Argentina, and never found anywhere else in South America, this species appears to be widely distributed in Australia (Greenslade & Najt 1987). Originating from the Australian region, it has been most probably, introduced into the Neotropics. *Brachystomella stachi* is known from the Nearctic and the Neotropical regions. *Brachystomella surendrai* is an Oriental species. *Brachystomella curvula, B. nubila, B. hiemalis, B. koreana* and *B. quadrituberculata* are known only from the Palaearctic region. *Brachystomella honda* is marine littoral and occurs in the south Nearctic and the north Neotropical regions.

Sixteen species originate from the Australian region: seven from Australian, five from the Hawaiian (*Brachystomella hawaiiensis, B. heo, B. kahakai, B. kiko* and *B. momona*), and three from the Polynesian (*B. perraulti, B. insulae, B. unguilonga*) subregions. Among these 16 species *Brachystomella fungicola* may represent another, probably new genus. *Brachystomella terrafolia* described from the New Zelandian subregion was reported also from India (Prabhoo 1971), but the specimens belong perhaps to a new species. Of the remaining 24 species, 22 are exclusively Neotropical and two are Ethiopian (from the South-African subregion).

The genus *Setanodosa* has 14 species (Table 3), eight belong to the Neotropical fauna, five to the Australian and one occurs in the Ethiopian and the Australian.

Table 3. Geographic distribution of species belonging to brachystomellian group (except *Brachystomella* sp.—see Table 2). Zoogeographic regions: Nea—Nearctic; Pal—Palearctic; Neo—Neotropical; Eth—Ethiopian; Ori—Oriental; Aus—Australian.

Species	Nea	Pal	Neo	Eth	Ori	Aus
Setanodosa Salmon, 1942						
afurcata (Womersley, 1933)						+
capitata (Womersley, 1930)				+		+
clavata (Schaeffer, 1897)			+			
decemoculata (Cassagnau & Rapoport, 1962)			+			
fueguensis Najt, 1973			+			
granulata (Womersley, 1935)						+
kanalua Christiansen & Bellinger, 1992						+
occidentalis (Arlé, 1959)			+			
peruensis Massoud, 1967			+			
quinseta Salmon, 1944						+
rosasi (Bonet, 1934)			+			
serrata Massoud, 1967			+			
steineni (Schaeffer, 1891)			+			
tetrabrachta Salmon, 1942						+
Micronella Arlé, 1959						
porcus (Denis, 1933)			+			
checayensis Massoud, 1967			+			
Probrachystomellides Weiner & Najt, 1991						
nicolaii Weiner & Najt, 1991				+		
Brachystomellides Arlé, 1959						
compositus Arlé, 1959			+			
geniculatus (Womersley, 1934)						+
micropilosus Cassagnau & Rapoport, 1962			+			
neuquensis Cassagnau & Rapoport, 1962			+			
Parastomella Rapoport & Rubio, 1968						
mylodontis Rapoport & Rubio, 1968			+			
Bonetella Stach, 1949						
terricola (Womersley, 1933)						+
Winterella Massoud, 1967						
arlesiana Massoud, 1967			+			
Subclavontella Stach, 1949						
acantha (Womersley, 1933)						+
subacantha Massoud, 1967						+
Folsomiella Bonet, 1930						
caeca (Folsom, 1927)			+			
albida (Arlé, 1959)			+			
intermedia (Arlé, 1939)			+			
nothofagutalis (Rapoport & Rubio, 1963)			+			
polylepiana Massoud, 1967			+			

Table 4. Geographic distribution of species belonging to rapoportelian group. Zoogeographic regions: Nea—Nearctic; Pal—Palearctic; Neo—Neotropical; Eth—Ethiopian; Ori—Oriental; Aus—Australian.

Species	Nea	Pal	Neo	Eth	Ori	Aus
Rapoportella Ellis & Bellinger, 1973						
bonariensis (Rapoport, 1962)			+			
boneti Massoud, 1963			+			
karta Greenslade & Najt, 1987						+
lowriei Najt, 1984			+			
margaritae Najt & Palacios-Vargas, 1986			+			
mucronata Najt & Massoud, 1974			+			
punillensis Izarra, 1973			+			
rapoporti (Massoud, 1963)			+			
sergioi (Najt, 1973)			+			
sigwalti Najt & Palacios-Vargas, 1986			+			
yolandae (Rapoport & Maño, 1969)			+			
Raponella Najt, 1988						
dodecophthalma (Rapoport & Rubio, 1963)			+			
Cassagnella Najt & Massoud, 1974						
alba Najt & Massoud, 1974			+			
anomala (Womersley, 1933)						+
Salvarella Greenslade & Najt, 1987						
wallacei Greenslade & Najt, 1987						+

The only species of *Micronella* are exclusively Neotropical. *Probrachystomellides nicolai* is monotypic, at present known only from South Africa, and thus belonging to the Ethiopian region. *Brachystomellides* includes four species, three in the Neotropical region and one in Australia. *Parastomella mylodontis,* described from Mylodon Cave in Chile, is monotypic and limited to the Neotropical region (Patagono-Andean subregion). *Bonetella terricola,* also a monotypic genus, is known only from the Australian region, and *Winterella arlesiana* from the Neotropics. *Subclavontella* is represented by two species in the Australian region. *Folsomiella,* with five species, is characteristic for the Central and South-American continent: the Neotropical region.

Within the brachystomellian group, only three species of *Brachystomella* are distributed over two and one in four geographical regions. Each of the remaining 77 species has its distribution restricted to a single biogeographic realm.

The rapoportellian group includes four genera: *Rapoportella, Raponella, Cassagnella* and *Salvarella* (Table 4). Ten species of the genus *Rapoportella* are Neotropical and one is Australian.

Raponella dodecophtalma is monotypic in the Neotropical region. *Cassagnella* contains two species, the Patagono-Andean *C. alba* and the Australian *C. anomala.* This latter species, characterized by elongated maxillae with lamellae, was orig-

inally described as belonging to the genus *Brachystomella* but according to Womersley (1939) this classification was incorrect. *Salvarella wallacei* is monotypic and known only from the Australian region. The rapoportellian group has no representatives in the Holarctic region.

Discussion and Conclusions

Only one of the 14 brachystomelline genera, *Brachystomella,* has a worldwide distribution; the occurrence of five genera is limited to the Neotropical region, three to the Australian region, and one to the Ethiopian region. Four genera occur in the Neotropical and the Australian regions.

Of the 98 known species of Brachystomellinae, three are from two and one from four regions. Among the remaining 94 species, 55 are characteristic of the Neotropical, 28 of the Australian, five of the Palaearctic, one of the Nearctic, three of the Ethiopian, one of the Ethiopian and Australian and one of the Oriental regions. Thus, both the greatest number of genera (as many as 10) and maximum of species diversity (57 species) are to be found in the Neotropical region.

Collembola, a sister group of insects, are known from the mid Devonian, from about 400 millions y.b.p. This panchronic group has survived all geological epochs without undergoing any basic change of its initial form. Their center of origin was doubtlessly located in Pangaea. Collembola have developed a variety of adaptations that allowed them not only to conquer all habitats but also invade various continents.

We postulate that the Brachystomellinae began with a Pangaean ancestor, and that the strongest diversification and the most intense speciation took place on Gondwana Land beginning from an ancestor of *Brachystomella* type. The original group: *Brachystomella,* survived unchanged on the continent of Laurasia, but Gondwana Land, isolated and drifting away, developed a variety of climates and habitats which allowed for an evolutionary explosion *in situ.* As we have shown above, Brachystomellinae are represented by a few species in the Holarctic region and only the genus *Brachystomella.* The same genus occurs throughout the Southern Hemisphere, where it has diversified into many species and also given origin to the proliferation of genera endemic to the Southern Hemisphere.

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